Texture segmentation without human "V4"

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Abstract

Texture segmentation, or 2nd-order segmentation is a rapid perceptual process, allowing object and surface boundaries to be effortlessly detected. It is currently unclear whether this is achieved in early cortical areas or whether it necessitates the region referred to as human V4. The present report presents a single case study of patient MS, whose bilateral occipitotemporal damage includes the putative human V4 area, yet whose early visual cortex is spared. As shown in these experiments, MS can accurately locate a target defined by an orientation contrast to its background, even with considerable orientation noise. Importantly, his performance was significantly reduced when the texture edges were masked by black borders (thus preventing edge-based segmentation), indicating that he retains a functional edge-based texture segmentation process. Additionally, when the sign of the orientation contrast was reversed at a temporal frequency of 12.5Hz, MS could nonetheless detect the contours defined by the orientation contrast despite being unable to judge whether the surfaces either side of the contrast were the same or not. This reveals that MS's early visual cortex is sufficient for the intact phase-insensitive component of texture segmentation. Human area V4, therefore, is not necessary for texture segmentation.

Keywords: texture, V4, segmentation, neuropsychology

Introduction

Texture segmentation, also termed 2nd-order segmentation, is the process by which the visual system rapidly detects a discontinuity in some 2nd-order property, allowing the localisation of complex boundaries between objects and surfaces. This is strongly believed to be edge-based (i.e. originating at the locations of contrast), in comparison to the region-based analyses that allow texture *discrimination.* One widely studied form of segmentation is that resulting from an orientation contrast – when two regions of orientations abut and differ in the mean orientation of their textural elements, a contour is effortlessly seen between the two regions. This process of edge-based texture segmentation is thought to be achieved first through the application of first order orientation-specific filters in the visual system, whose outputs are then transformed through a second stage non-linearity. A final stage of linear filtering is then conducted on this output with larger receptive fields than those of the first, and is sensitive to the location of any spatial gradient in the orientation-defined texture (see Bergen, 1991, for a detailed review of such a model).

Despite substantial efforts, it has been difficult to isolate the cortical regions that are involved in this process. One candidate area is the earliest possible cortical stage of visual processing – primary visual cortex (V1). This is seen as a likely substrate for at least the linear filtering stage of texture segmentation, due in part to its extensive network of simple and complex cells, and the presence of both excitatory and inhibitory lateral interactions, which may be sufficient to implement even 2nd-order non-linearities (Landy & Graham, 2004). Indeed, single-cell recordings in the macaque revealed the activity of V1 cells in response to an oriented line or texture to be enhanced by the presence of an orthogonal surround (Knierim & van Essen, 1992; Sillito, Grieve, Jones, Cudeiro & Davis, 1995), whereas activity was suppressed for homogenous regions (Nothdurft, Gallant & van Essen, 2000). Importantly, some researchers have suggested that V1 is sufficient in this role; when extrastriate areas are ablated or suppressed, cell responses in V1 to texture borders do not diminish (Lamme, Supèr, & Spekreijse, 1998; Lamme, Rodriguez-Rodriguez & Spekreise, 1999; Hupé, James, Girard & Bullier, 2001). Primary visual cortex, therefore, may play a sufficient role in texture segmentation. It should be noted, however, that these results only support edge-detection, and not necessarily the assignment of figure and ground, being achieved in the initial feedforward sweep from V1 to higher areas. The neural model of

segmentation proposed by Lamme (Lamme *et al*, 1998; 1999), for instance, does propose that feedback from higher visual areas is necessary to assign the properties of figure and ground to surfaces, but not in the detection of contours arising from spatial gradients in texture.

This view is not, however, without its critics; neuroimaging evidence in particular has revealed that the blood-oxygen-level-dependent (BOLD) response in early visual areas (specifically V1 and V2) either not to be correlated with the degree of contrast of a texture-defined figure or to be much weaker than that in later areas (Kastner, de Weerd and Ungerleider, 2000; Larsson, Landy & Heeger, 2006[1]; Montaser-Kouhsari, Landy, Heeger & Larsson, 2007; Thielscher, Kolle, Neumann, Spitzer & Gron, 2008). Typically, the activity is observed in an area described as human V4, and some have directly speculated that the segmentation process depends on recurrent activity between this area and lower-level areas, with the final representation of the segmentation occurring in V4 (Thielscher *et al*, 2008). Computational neuroscience has attempted to further our understanding of this process, specifically by modelling V1, V2 and V4 cells together in an interactive network such that selective artificial "lesions" can be induced and the resulting activity in these regions can be observed in response to stimuli that require 2nd-order segmentation (Thielscher and Neumann, 2007). With the removal of feedback connections from V4 to V2, the neural representation of a region defined by an orientation contrast in the presence of orientation noise is suppressed at the level of V2 (Thielscher & Neumann, 2005), further supporting the view that V4 is necessary for segmentation. It is, of course, difficult to extrapolate the results of such computational modelling studies and apply them to the human visual system, but many properties of the cells in those computational models, such as their receptive field size and response latency, are indeed based on data obtained from functional imaging studies (e.g. Smith, Singh, Williams & Greenlee, 2001). Studies focussing on the impairments following human lesions are, therefore, needed in order to determine if higher cortical areas are necessary for texture segmentation. One neuropsychology patient (HJA), with damage to V4, is impaired both in segmenting a single bar defined by an orientation contrast to its background (Allen, Humphreys, Colin & Neumann, 2009) and in estimating the average orientation of a set of line segments (Allen, Humphreys & Bridge,

[1] Larsson *et al* (2006) reported only a trend for progressively greater activity from V1 to V4.

2007). This patient, however, also has damage to earlier areas V2 and V3, and although a region-based signal-pooling process such as orientation averaging is likely to depend on V4, it remains unclear whether earlier cortical areas may in fact be sufficient for edge-based texture segmentation.

It is important to note at this point that determining the true human homologue of macaque area V4 is difficult. Area V4 in the monkey was initially referred to as a "colour area" (Zeki, 1973, 1983, 1990; Walsh, Butler, Carden & Kulikowski, 1993) and the observation in humans that an area in the vicinity of the lingual and fusiform gyri responded selectively to chromatic stimuli (Zeki *et al* 1991), and that damage within this area resulted in achromatopsia (Heywood, Cowey & Newcombe, 1991), led to the classification of this particular area as human V4. Surgical lesions of macaque V4, however, did not reveal a comparable animal model of achromatopsia, instead producing significant deficits in form perception (Heywood, Gadotti & Cowey, 1992; Heywood & Cowey, 1987), casting doubt on its colour selectivity and thus on its putative relation with human V4. See also Roe et al (2012) for a comprehensive review of the function of V4 along with a discussion of the existence of a human V4 that is comparable to that found in the monkey brain. It is also contended through neuroimaging evidence that the human colour centre is distinct from area V4 (Hadjikhani, Liu, Dale, Cavanagh & Tootell, 1998), possibly in VO-1 or VO-2 (Brewer, Liu, Wade & Wandell, 2005) or in an area more anterior (Murphey, Yoshor & Beauchamp, 2008). See Winawer and Witthoft (2015) for a recent summary of the location of human V4 and, in particular, the distinction between this area and the VO maps. The reference to human V4 in the present study is made with the intention to relate to the terminology of others who have conducted related studies of texture segmentation with human observers (e.g. Thielscher *et al*, 2008; Thielscher & Neumann, 2007; Allen *et al*, 2009; Kastner *et al*, 2000). The region in question is comparable on anatomical grounds to that identified by McKeefry and Zeki (1997), being situated on the collateral sulcus of the fusiform gyrus.

The purpose of the present study was to develop our understanding of the role of area V4 in texture segmentation, by testing the performance of a single patient (MS), who has bilateral damage to his ventromedial occipitotemporal cortices that includes the area often identified as human V4. Damage to his early visual cortex (at least in one hemisphere) is relatively spared. MS, therefore, provides a good neuropsychological test of the role of human V4 in texture segmentation. In the present study, patient MS performed an oddity-

detection task, in which he had to indicate which of three texture patches contained a target subregion defined by an orientation contrast. His performance was also measured with the presence of coincident black border masks at the locations of orientation contrast, thus attenuating edge-based segmentation cues. As shown in Norman, Heywood and Kentridge (2011), such coincident border masks selectively impair edge-based segmentation processes, leaving other region-based processes unaffected. Specifically, when participants were required to detect a target region defined by a spatial gradient in mean orientation, their performance was consistently impaired with the inclusion of border masks, but when they detected a target defined by a spatial gradient in orientation variance (which does not induce a perception of a contour) their performance was unaffected. In the present study, if MS's intact brain regions allow him to segment the target using edge-based segmentation cues, then his performance should be consistently better when the border masks are absent than when they are present. In experiments one and two, MS's performance on both versions of the task was measured psychophysically by varying task difficulty. This was done by varying the degree of orientation flow in the stimuli (i.e. by what degree the individual orientations were rotated clockwise as one moved rightwards and downwards through each texture pattern).

General methods

Subject

Patient MS has bilateral damage to his ventromedial occipitotemporal cortex and is profoundly achromatopsic and prosopagnosic as well as having visual object agnosia. Damage to the left hemisphere includes the temporal pole, parahippocampal and fourth temporal gyri of the temporal lobe, the collateral sulcus, and the mesial occipitotemporal junction. His achromatopsia is most likely explained by the damage to the lingual gyrus and anterior collateral sulcus, typically associated with human V4. Damage in this vicinity is also likely to be the cause of his impairment in discriminating surface properties of objects more generally (Cavina-Pratesi, Kentridge, Heywood & Milner, 2010a, 2010b) along with his prosopagnosia. His ability to perceive object form remains intact, which is likely the result of his spared lateral occipital complex (LOC; Cavina-Pratesi *et al,* 2010b). Retinotopic mapping has not been successfully carried out in patient MS, so it is difficult to say with

certainty which visual fields remain intact in this left hemisphere. It is clear that V1 is spared and possibly parts of V2 (second visual area), but given the extensive damage to his lingual gyrus, it is unlikely that V3 (third visual area) is intact and certain that V4 (fourth visual area) is not. The damage in his right hemisphere is more extensive than that in the left, including primary visual cortex resulting in a homonymous hemianopia with macular sparing, whereas his occipital lobe in his left hemisphere is largely intact. For a more extensive case description of MS, see Heywood, Cowey and Newcombe (1994) and a structural MRI scan of MS's brain, revealing the extent of his cortical damage, can be found in figure 1 of Heywood, Cowey & Newcombe (1991) and in figure 1 of Heywood *et al* (1994). Testing was conducted over the course of two days at the University of Durham's Psychology Department. MS was 63 years of age at the time of testing.

Stimuli

MS viewed the display monitor at a distance of approximately 80cm. Stimuli were presented on the uniform grey background (50 cdm^{-2}) of a gamma-corrected ViewSonic 17'' (1254 x 877 pixels) colour monitor driven by a Cambridge Research Systems VSG 2/5 Graphics System running at 100Hz.

Stimuli consisted of three separate textures of 10 x 10 Gabor patches (Michelson contrast of 90%). Each Gabor patch measured 0.7° in diameter, with a spatial frequency of 1.4 cyc/° and an envelope with a standard deviation of 0.2°. Each Gabor patch was separated from its neighbours by 0.3°. Thus, each texture measured 9.7° in width and in height. The phase of each Gabor patch was determined randomly and independently from the full 360° cycle. The three patches were aligned vertically in the centre of the display, with a distance of 1.4° separating each of the top and bottom patches from the middle. See **figure 1** for an illustration of the stimuli. MS was allowed full free-viewing of the stimuli in order to account for his left hemianopia.

Experiment 1 – 2nd-order segmentation in patient MS

Methods

Three levels of task difficulty were included and randomised throughout each block of trials; the difficulty was determined by the degree of orientation flow within the three

textures. That is, the degree to which the orientation of each Gabor patch was tilted relative to those immediately above and to the left, originating at the uppermost and leftmost Gabor patch (which was set at horizontal). Thus the orientation of each Gabor patch (*g*) at location (*i j*) is represented in the following function:

$$g_{(i,j)} = a + b(i-1) + b(j-1)$$

Where *a* represents the starting orientation, *b* represents the degree of orientation flow and *i* and *j* represent the horizontal and vertical positions of the Gabor patch, respectively. For this experiment, all three textures began with a horizontal orientation (a=90), and three levels of orientation flow were used: b=0° (no flow), 8° (small flow) or 15° (large flow). In addition, each individual Gabor patch's orientation was drawn from a Gaussian distribution with a standard deviation of 5°, thus introducing a small amount of baseline orientation noise, and this was done *de novo* on each trial.

In each trial, one of the textures (either the top or bottom, chosen randomly with equal probability) was constructed differently to the others, by offsetting the central 6 x 6 square region of Gabor patches by 90°. In half of the blocks of trials, the central 6 x 6 region in all three textures was surrounded by a black border mask 0.2° in thickness, thus attenuating the perception of the target's contours. Patient MS conducted ten blocks of trials: five with the border masks absent and 5 with the border masks present. The two block types were conducted in alternation, and within each block, 10 repetitions of each of the three flow pattern levels were randomly interleaved, amounting to 30 trials per block. The stimuli remained onscreen until MS indicated which patch (the top or bottom) appeared to be the odd-one-out (i.e. which contained the central 6 x 6 target). Patient MS verbalised his response and the experimenter pressed the corresponding key on a response box to proceed to the next trial. Examples of the types of stimuli are shown in **figure 1**.

Results

MS's accuracy was compared to that of chance performance using binomial tests. For each level of orientation flow (0°, 8° and 15° respectively), MS's performance without the border masks was significantly above chance: 50/50 (100%; $p<0.001$), 46/50 (92%; $p<0.001$) and 38/50 (76%; $p<0.001$). Similarly, his performance with the border masks was also above chance: 47/50 (94%; $p<0.001$), 32/50 (68%; $p = 0.032$) and 32/50 (68%; p =

0.032). To compare MS's performance with and without the presence of the border masks, the three difficulty levels were collapsed, and overall MS performed better without the border masks ($\chi^2_{(1)}$ = 11.78, p<0.001). Results are illustrated in **figure 2a**. Individual comparisons at each level of difficulty show that MS performed better without the border masks only in the intermediate difficulty condition ($\chi^2_{(1)}$ = 11.42, p<0.001), but not the low ($\chi^2_{(1)}$ = 3.09, p=0.079) or high ($\chi^2_{(1)}$ = 1.71, p = 0.190) conditions, compared to when the masks were present.

A two-way ANOVA, with the factors border mask (present, absent) and orientation flow (0°, 8°, 15°), on MS's response times revealed there was no significant difference in his time to respond when the border masks were absent compared to when they were present ($F_{(1,294)}$ = 1.641, p = 0.201). There was, however, a significant effect of orientation flow ($F_{(2,294)}$ = 13.637, p < 0.001), with response times being shorter for 0° (mean = 7.778 s) compared to 8° (mean = 13.298 s, p < 0.001) and 15° (mean = 13.859 s, p < 0.001) level of orientation flow. There was no interaction between the two factors ($F_{(2,294)}$ = 2.262, p = 0.106). Overall these response time data do not provide any evidence of a speed-accuracy trade-off in MS's detection of the odd texture.

Interim discussion

MS's ability in the previous experiment to detect regions defined by orientation contrast was less accurate when border masks were present at the locations of contrast compared to when they were absent, although this ability was nonetheless above chance. It could be argued, however, that MS was completing this task using only local cues, by attending to and comparing only the top-left orientation, for example, within the 6 x 6 target region of each of the three textures. Experiment 2, therefore, was designed to prevent the use of such local cues, and thus to test more appropriately MS's ability to detect regions defined by orientation contrast both with and without the presence of border masks. This was done by assigning each of the three textures with a unique starting orientation, thus ensuring that it was not possible to infer the location of the target region from one single orientation within the target region.

Experiment 2 – 2nd-order segmentation in patient MS without local orientation cues

Methods

The stimuli and methods were identical to experiment 1, except that for each trial a random value from the full 360° cycle was chosen and was assigned as the starting orientation for one of the textures. Of the remaining two textures, one was chosen to have a starting value 45° clockwise from this value, and the other 90°, and the positions of these three textures were randomly allocated in the vertical array. Thus, each texture assumed different background orientations to the other two, and the odd-one-out corresponded to the one whose target region did not agree with the continuity of the background. This task could not be accomplished using local cues.

Results

For each level of orientation flow (0°, 8° and 15° respectively), MS's accuracy without the border masks was significantly above chance: 45/50 (90%; $p<0.001$), 42/50 (84%; $p<0.001$) and 42/50 (84%; $p<0.001$). His accuracy with the border masks was also above chance in the two least difficult conditions, 38/50 (76%; $p<0.001$) and 34/50 (68%; $p = 0.008$), but not in the most difficult condition, 30/50 (60%; $p = 0.101$). To compare MS's accuracy with and without the border masks the three difficulty levels were collapsed, and it was found that overall MS performed better when the border masks were absent compared to when they were present ($\chi^2_{(1)} = 13.72$, $p < 0.001$). Results are illustrated in **figure 2b**. Individual comparisons at each level of difficulty show that MS performed better without the border masks only in the high difficulty condition ($\chi^2_{(1)} = 7.14$, $p = 0.007$), but not the low ($\chi^2_{(1)} = 3.47$, $p=0.062$) or intermediate ($\chi^2_{(1)} = 3.51$, $p = 0.061$) conditions, compared to when the masks were present.

A two-way ANOVA, with the factors border mask (present, absent) and orientation flow (0°, 8°, 15°), on MS's response times revealed that his time to response when the border masks were absent (mean = 8.840 s) was significantly shorter compared to when they were present (mean = 13.228; $F_{(1,294)} = 15.035$, $p < 0.001$). There was, however, no significant effect of orientation flow ($F_{(2,294)} = 0.636$, $p = 0.530$) and no interaction between the two factors ($F_{(2,294)} = 1.739$, $p = 0.177$). As with experiment one, these response time

data do not provide any evidence of a speed-accuracy trade-off in MS's detection of the odd texture.

Interim discussion

In the previous experiments, MS's ability to detect a region defined by orientation contrast was consistently more accurate when there were no coincident black borders to mask his perception of the contours. This implies that MS was using the orientation contrast to inform his judgment and was not relying solely on a technique of region-based texture analysis. This was also true for stimuli in which there was a considerable degree of orientation noise, suggesting that, contrary to what has been implied through computational modelling (Thielscher & Neumann, 2003), V4 is not required for segmentation of even complex 2nd-order stimuli.

The mammalian visual system gives temporal priority to edge-based cues, relative to region-based cues – there is an early cellular response corresponding to the location of a border, for example, compared to the location of a texture surface (Lamme *et al,* 1999; Romani, Caputo, Callieco, Schintone and Cosi, 1999). Many psychophysical experiments in humans also lend weight to the idea of a temporal dissociation between edge- and region-based processes (e.g. Motoyoshi, 1999), and together imply that very early, rapid mechanisms underlie edge-based segmentation. Another important aspect of edge-based segmentation is that it is phase-insensitive – that is, the texture border is encoded independently of the direction of orientation contrast across the border (Norman *et al,* 2011). When the orientations in the background and target regions alternate at a rapid rate, for example, segmentation is still possible because the magnitude of the contrast is kept constant despite the inconstant phase (or direction of orientation contrast). As experiments one and two did not directly address this important aspect of segmentation, experiment 3 was designed to test MS's segmentation ability using rapid orientation-reversing stimuli (Norman *et al,* 2011). In the following experiment the orientations in the target and background regions alternated at a frequency of 12.5Hz. At approximately this frequency level in normal observers, the ability to segment a region defined by orientation contrast persists but the ability to judge whether the regions either side of the contour are different is likely to be lost or severely impaired, revealing a phase-insensitive component to

segmentation (Norman *et al*, 2011). Demonstrating that MS could successfully use the edge-based segmentation cues in these stimuli, whilst being unable to discriminate the regions he was segmenting, would substantially strengthen the claim that MS's ability to perform texture segmentation is intact.

Experiment 3 – phase-insensitive 2nd-order segmentation in patient MS

Subjects

Along with patient MS, 3 male control participants (mean age: 30.3 years, standard deviation: 1.3) with no visual disorders were also tested in experiment 3.

Methods

Stimuli were constructed in the same way as in experiment 1, although the level of orientation flow was not manipulated (set at 0°). Stimuli were presented onscreen following a brief mask (30 ms) consisting of three textures of random orientations. The orientations of the test stimuli then reversed at a frequency of 12.5Hz between vertical and horizontal (the orientation reversal occurred every 40 ms). See **figure 3** for a depiction of the stimuli. This persisted until MS made a response. Four blocks were conducted; two of which included border masks and two of which did not, and each block contained 25 trials.

Results

MS performed significantly above chance without the presence of border masks, with 38/50 hits (76%; $p < 0.001$), which is in stark contrast to his performance with the presence of the border masks, which remained at chance (26/50 hits, 52%; $p = 0.444$). His performance was statistically greater when the border masks were absent ($\chi^2_{(1)} = 6.25$, $p = 0.012$) compared to when they were present. Results are illustrated in **figure 2c.**

A t-test revealed that there was no difference in MS's time to respond when the border masks were present (mean = 10.486) compared to when they were absent (mean = 12.353; $t_{(98)} = 0.875$, $p = 0.384$). As with experiments one and two, these response time data do not provide any evidence of a speed-accuracy trade-off in MS's detection of the odd texture.

Data from each of the three control participants were analysed in the same manner as those from MS. The three control participants performed significantly above chance without the border masks, each with 49/50 hits (98%, $p < 0.001$). Without the border masks the performance of two of the participants was each not statistically better than chance, with 27/50 hits (54%, $p = 0.336$) and 28/50 hits (56%, $p = 0.240$). The remaining participant was marginally better than chance, with 32/50 hits (64%, $p = 0.032$). Overall these results suggest that the inclusion of the border masks around the target region significantly impaired participants' ability to detect that target region, and this is a similar pattern of results to that shown in patient MS. Comparing the very high hit rates obtained when the border masks were absent compared to when they were present suggests that the orientation reversal of 12.5 Hz was sufficiently high to strongly mask the perception of the Gabor patches' orientations but not the contrast between them at the target's contour.

General discussion

If MS's damaged cortex were responsible for edge-based texture segmentation, then he should be unable to use edge-based cues to detect a surface defined by an orientation contrast. In experiments one and two this was clearly shown not to be the case – MS achieved close to 100% accuracy in the simplest segmentation task (no orientation flow) when edge-based cues were available to him. Even when a large degree of orientation flow was introduced to the stimuli, which requires more complex analyses (Thielscher & Neumann, 2007), MS's accuracy in the segmentation condition did not fall below 75%. These results strengthen the claims that human area V4 is not necessary for texture segmentation and that early cortical areas are likely to be sufficient.

Is it possible, however, that MS did not rely on a truly edge-based segmentation mechanism to perform this task, instead relying on a more effortful region-based mechanism? Previous psychophysical work has identified at least two mechanisms of texture perception – one that originates from the contour between two adjacent textures, and another that involves a region-based analysis of the texture surfaces (Wolfson and Landy, 1998). Although these are considered to be dissociable processes, human observers have been shown to use a hybrid of the two when performing tasks of texture segmentation

(Mumford, Kosslyn, Hillger & Herrnstein, 1987). It is important, therefore, to identify the mechanism underlying MS's preserved segmentation ability. The most parsimonious interpretation of the results of experiments one and two is that he was indeed using edge-based segmentation – when the contours of the target region were masked by black borders MS performed the task with significantly less accuracy, albeit still above chance in most cases. This indicates that his perception of the target was aided by the contrast information present at the location of the contours. It cannot be claimed, therefore, that he was using a purely region-based mechanism (i.e. scrutinising individual orientations of target and background) in order discern the location of the target in the segmentation conditions, as his performance would have been unaffected by the presence of the border masks if this were the case. It is noted, however, that the effect of orientation flow in experiment 1 appears to have been more substantial than in experiment 2. It is possible, therefore, that MS relied on some scrutiny of local orientation cues in experiment 1 but, with the use of variable starting orientations in experiment 2, was prevented from doing so in experiment 2. Overall, however, the results of the first two experiments do support the notion that MS is capable of at least some edge-based texture segmentation, as he performed consistently more accurately when the contour cues were available to him.

Furthermore, experiment three strongly suggests that MS's segmentation is very rapid, as he was able to identify the target even when the orientations of the background and target elements alternated at a frequency of 12.5Hz (40 ms per stimulus frame). In normal observers at approximately this frequency, the background and target surfaces become indistinguishable from one another, yet the perception of a contour between the two is strong and segmentation still occurs (Norman *et al*, 2011). MS showed this same pattern of results; he was at chance when the contours were masked, yet he could accurately identify the target when the contours were not masked. Thus, despite the strict temporal limit imposed upon the processing of the stimuli, MS was nonetheless able to detect the contours defined by the orientation contrast. This implies that MS has an intact 2^{nd}-order segmentation mechanism that can detect the presence of texture boundaries within a period of 40 ms even when the stimulus is both forward- and backward-masked (as ensured by the method of phase-reversing). We are unable to comment, however, on the time-course of the subsequent perceptual stages that would integrate these consecutive 2^{nd}-order contrast signals over time, as these mechanisms would be phase-insensitive and

therefore may rely on a wider temporal integration window. Overall, the results of the experiments show that it is very unlikely that MS was relying on a method other than an edge-based mechanism to achieve texture segmentation. It should be noted, however, that this result does not imply that MS has a fully intact ability to segregate figure from ground – only that MS is able to detect a contour between two regions that differ in some 2nd-order attribute.

These results shed new light on the neural processes underlying texture segmentation. Specifically, they provide strong evidence that texture segmentation (by orientation contrast at least) does not necessarily depend upon the areas that are damaged in MS, specifically what is considered area V4. This contradicts earlier evidence from neuroimaging studies (Thielscher *et al,* 2008; Kastner *et al,* 2000) and computational modelling (Thielscher *et al,* 2007), which have led to the theory that V4 is necessary for segmenting figures defined by an orientation contrast, with specific emphasis on its role in providing feedback to lower areas and in ultimately representing the outcome of the segmentation process. The new results do, however, corroborate evidence from earlier cell-recordings in non-human studies, which indicated primary visual cortex to be sufficient for segmentation (e.g. Lamme *et al,* 1998; 1999; Hupé *et al,* 2001), although these cell-recording studies only support the claim that edge-detection, not necessarily the assignment of figure and ground, is achieved in the initial feedforward sweep from V1. Recently, Hallum, Landy and Heeger (2011) provided evidence from functional magnetic resonance adaptation showing populations of neurons within V1 to be sensitive to 2nd-order contrast, with the observed activity reflecting a two-stage filter process with surround suppression from 1st-order filters. As they found comparable stimulus-specific adaptation throughout V1-V4, they conclude that this activity was the result of feed-forward activity from V1.

Cells within V1 are known to process chromatic contrast (Kentridge, Heywood & Weiskrantz, 2007), which are highly likely to underlie MS's preserved ability to perceive form on the basis of such information. MS is, however, entirely blind to surface colour (Heywood *et al*, 1991), and functional neuroimaging has confirmed that the perception of this attribute in neurotypical controls indeed requires some of the anterior cortical areas that are damaged in MS (within the lingual gyrus and anterior collateral sulcus; Cavina-Pratesi *et al*, 2010b). As MS retains a generally good ability to discriminate regions of

orientations when the borders are masked in the present study, it is clear that his perception of the stimuli is not entirely analagous to his colour perception. It is likely that his spared ability to discriminate mean orientation is mediated by the orientation-selective cells within V1. Patient MS's ability to form more complex global representations based on distributed local orientation is, however, clearly impaired as he is unable to visually discriminate material textures (Cavina-Pratesi *et al*, 2010a; 2010b). The term integrative agnosia was introduced to describe the condition of a patient similar to MS (HJA), in which a prominent symptom is the impairment in representing configural stimulus information (Riddoch & Humphreys, 1987). Such an impairment would impact many aspects of perception, from pattern recognition to face perception. It is clear from previous tests on patients MS and HJA, however, that, despite their extensive occipitotemporal damage, neither patient is completely unable to integrate spatially distributed elements – HJA is somewhat spared at estimating mean orientation (Allen *et al,* 2007) and MS can even discriminate levels of orientation variance (Norman, Heywood & Kentridge, 2015). Such results imply that the visual system's ability to represent global attributes through the spatial integration of local elements is unlikely to have a single clear neural substrate, and areas as early as V1 and V2 are possibly sufficient for some basic region-based representations. What is clear from the present results, however, is that the mechanisms required for edge-based texture segmentation do not require the extrastrate area human V4.

Primary visual cortex is, however, not unique in its apparent sensitivity to texture contrast, and from the current results it is not possible to truly conclude that it is solely primary visual cortex that is responsible for MS's segmentation ability. Specifically, the second cortical visual area (V2), which lies immediately adjacent to V1 and with which it is largely interconnected, may play an important role in segmentation and it is possible that at least part of this area may be preserved and functional in MS's left hemisphere. Schira, Fahle, Donner, Kraft and Brandt (2004) showed that the BOLD activity in V2, although not V1, correlated with the contour of a figure defined by an orientation contrast, and they hypothesised that the observed activity in mid- to high-level areas merely reflected the feedforward activity from V2. Importantly, in their study, subjects completed an attentionally demanding foveal letter discrimination task and as a result the segmenting stimuli did not reach awareness. The activity they found, therefore, is likely to reflect the

preattentive processes involved in segmentation. Schira *et al* (2004) also focussed their analysis only on the retinotopic region associated with the texture *contour*, enabling them to more accurately relate the observed activity to the processes of edge-based segmentation rather than the more general processes associated with figure perception. V2 cells, both at the individual and population level, also respond well to complex shape information (Hegdé & Van Essen, 2000, 2003) and in a way that evolves relatively quickly (as early as 40 ms of stimulus exposure; Hegdé & Van Essen, 2004). This is largely upheld by the finding that lesions of V2 produce significant impairments in segmenting a texture-defined figure (Merigan, Nealey & Maunsell, 1993), in which the orientation of a figure comprising a subset of line segments of different orientations to their background could not be discriminated, whereas the same figure defined by colour or size could be.

It is also important to address the role of LOC, which is functionally spared in MS (Cavina-Pratesi *et al*, 2010a; 2010b), in the perception of a target defined by 2nd-order segmentation, which has been identified as a potential correlate, along with V4, in some neuroimaging experiments (e.g. Thielscher *et al,* 2008; Larsson *et al*, 2005). The role of this area has been extensively studied and seems to represent a neural correlate of the perception of object shape seemingly regardless of how the shape is defined (e.g. Kourtzi & Kanwisher, 2001; Tyler, Likova & Wade, 2004). In the present study, however, MS was not required to make any discrimination of the form of the target; the task required only its localisation. It is likely, therefore, that this task could be achieved independently of the LOC, and that the activity observed in this region in neuroimaging studies is not directly a result of the segmentation process *per se*, but instead reflects that of an integration stage for the purposes of form perception beyond the early- to mid-cortical processing hierarchy (Thielscher *et al,* 2008). This is a notion that may be indirectly supported by monkey lesions; Merigan (2000) lesioned area V4 in monkeys, an area which shows many processing characteristics not unlike those of LOC in humans and is thus not homologous to the human V4 discussed here, and demonstrated that the ability to segment two abutting regions of orientation orthogonal to one another was preserved. The same animals could not, however, identify the orientation of a bar defined by the same orientation contrast. This may suggest that their segmentation mechanism was intact, but their ability to integrate this information to perceive form was not.

In conclusion, the results from these experiments with patient MS provide compelling evidence that human V4 is not necessary for texture segmentation. In contrast, populations of neurons within primary visual cortex may be sufficient, although it is not known yet exactly how they might achieve this.

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Figures

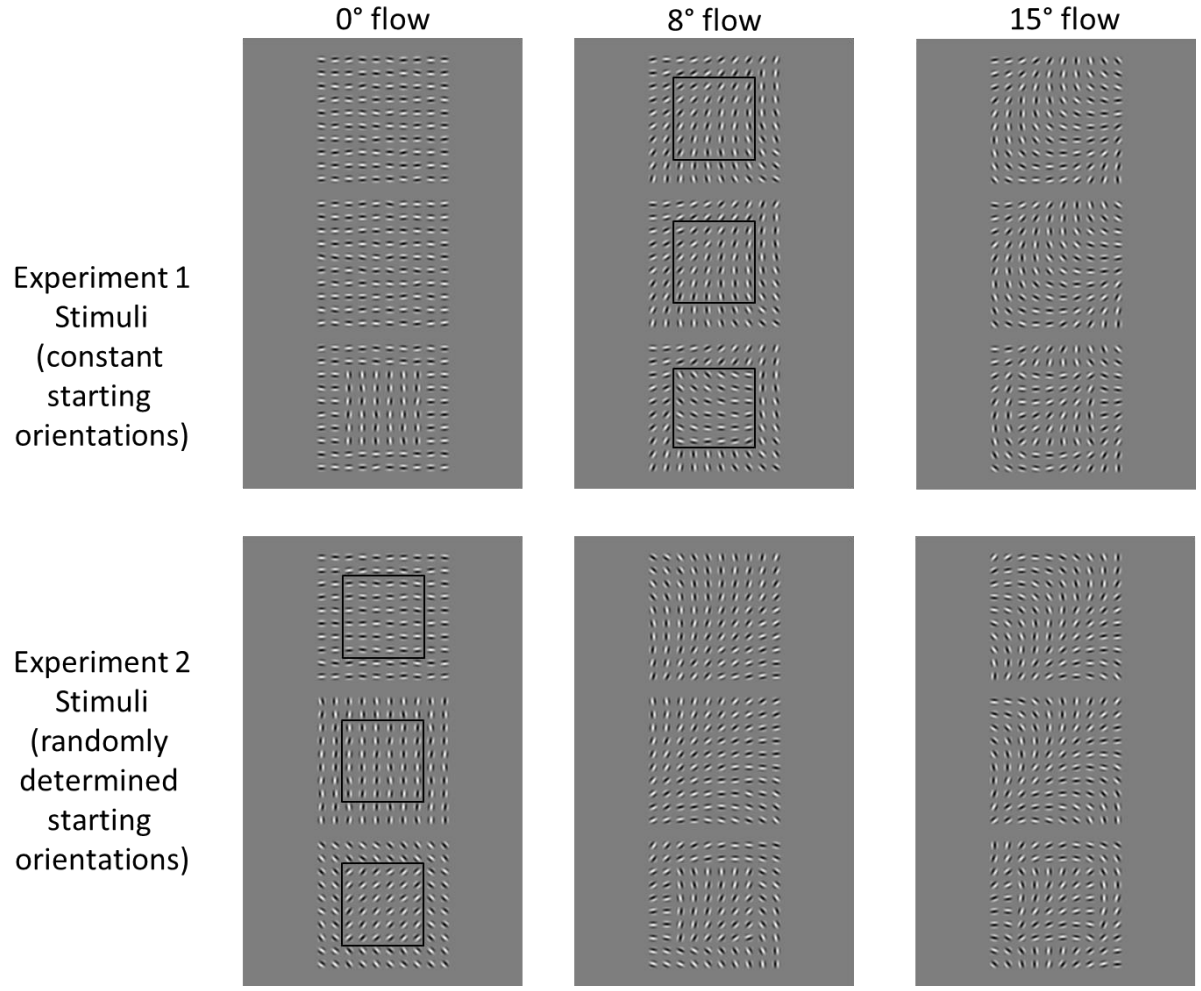

Figure 1 Illustration of the stimuli used in the the first two experiments (top row: experiment 1; bottom row: experiment 2). From left to right, the stimuli increase in the degree of orientation flow. In experiment 1, the starting value of the orientation flow was the same for the three textures (90°, plus or minus a small amount of normally distributed noise that was applied to each Gabor patch; see experiment 1 methods). In experiment 2, starting values were randomly allocated to the three textures (each offset by 45° different relative to the other two), thus removing the possibility of completing the task using purely local cues. Two of the images show examples of the stimuli with the inclusion of black border masks, in which the edge-based segmentation of the target is masked. Accurate performance in this condition requires greater analysis of the target and background regions. If MS is unable to use edge-based cues, however, then his performance should be similar with and without the border masks. MS's task was to detect which texture (top or bottom only) was the odd-one-out. Note that the black borders shown in this figure were subsequently manually added to the images of the Gabor patches so only approximately represent their appearance in the experiment.

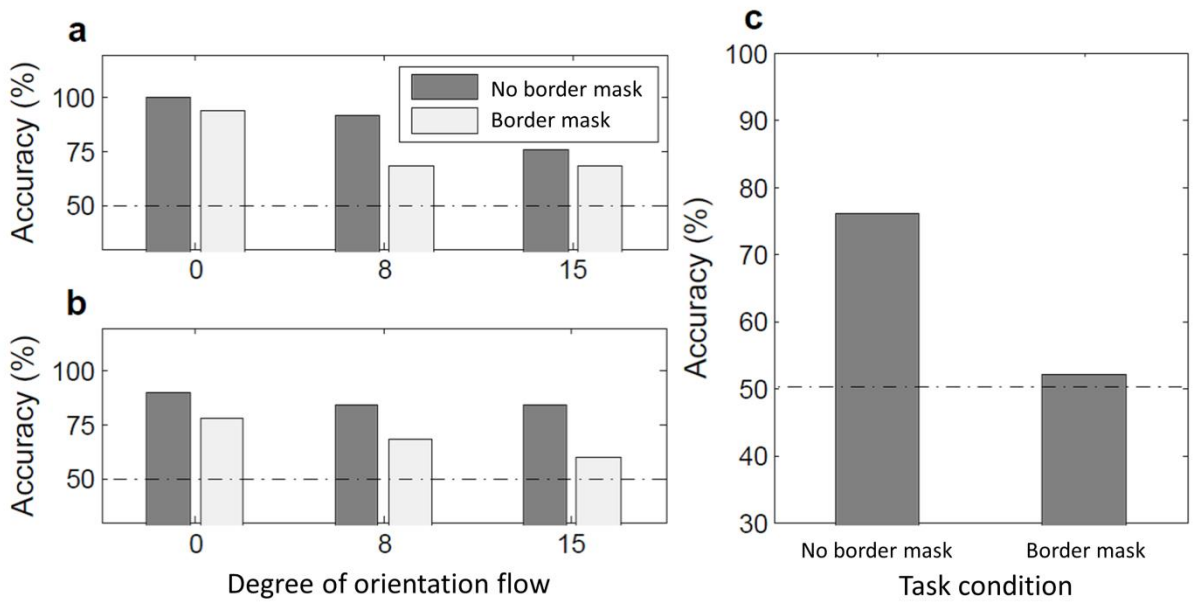

Figure 2 MS's accuracy (%) in experiments 1 (a), 2 (b) and 3 (c). In experiments 1 and 2, MS was able to detect the target more accurately when black border masks were not present compared to when they were present. In experiment 3, when the orientations of the target and background regions alternated at a frequency of 12.5Hz, MS was still able to detect the target without the border masks (76% correct), whereas he was unable to do this above chance when the border masks were present (52% correct). Together, these results indicate that MS has an intact ability to segment a target defined by an orientation contrast using edge-based mechanisms.

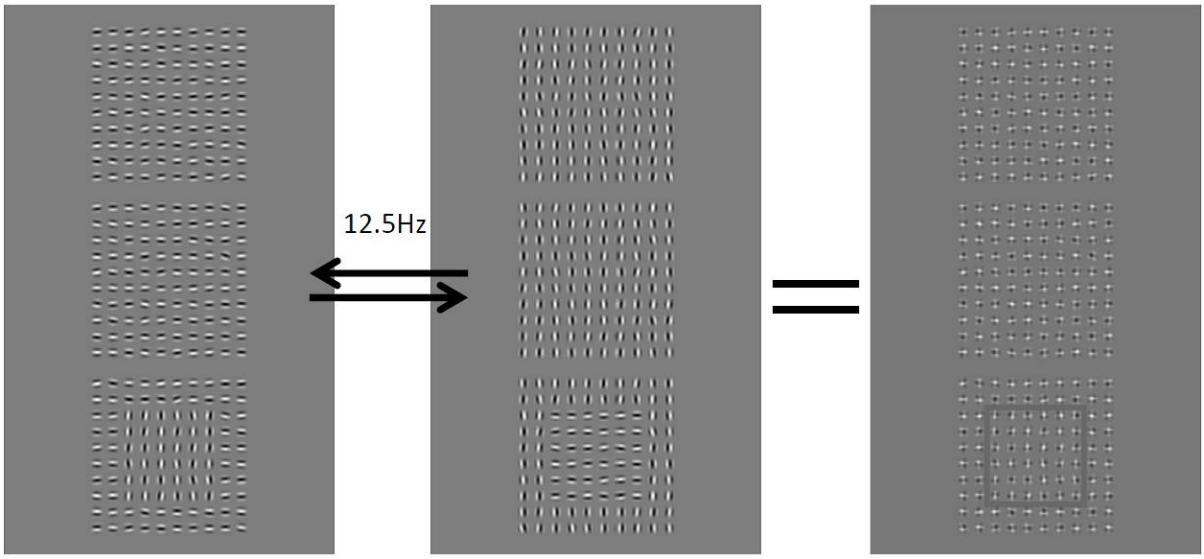

Figure 3 Illustration of the orientation-reversing procedure used in experiment 3. The target is defined by an orientation contrast of 90°, but the phase of this contrast is reversed at a frequency of 12.5 Hz. The resultant perception is illustrated in the rightmost illustration panel; the target and background surfaces appear identical yet the perception of an "illusory" contour is present around the target (as a result of the rapid segmentation process that may be phase-insensitive). MS's task, again, was to detect which texture was the odd-one-out. He also completed a version in which black border masks were present (see **figure 1** for an example).